

THE MECHANISM OF BURROWING IN THE POLYCHAETE WORM, *ARENICOLA MARINA* (L.)

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New techniques of recording pressure changes and activity have increased our knowledge of the fluid dynamics of burrowing in *Arenicola marina* (L.) (Trueman, 1966a). The new information, together with an understanding of the habits of the lugworm, derived from the extensive researches of Wells (1961), allow an assessment of the mechanism of burrowing to be made.

Initial entry of a worm into sand is brought about by the eversion of the proboscis at comparatively low coelomic pressures (2–6 cm. water pressure) and when several segments have passed beneath the surface a series of pressure peaks commence, each of about two seconds duration. They occur at intervals of 5–7 seconds, and as burrowing progresses increase in amplitude up to 110 cm. During burrowing, waves of peristaltic contraction pass along the trunk from the posterior segments to the anterior buried region of the worm where they appear to develop into high pressure peaks by the synchronous contraction of the longitudinal muscles of all or part of the trunk segments. The fluid of the essentially single trunk coelom acts in a hydraulic system which allows the force produced by the longitudinal muscles of the posterior trunk to be transferred to the anterior end, there to be utilized in burrowing. The principal function of the high pressure is to anchor the anterior end during the contraction of the longitudinal muscles. Each time the pressure increases the anterior end is pressed firmly against the substrate, while the posterior trunk is pulled into the burrow.

The purpose of this article is to consider further observations of the movements made by *Arenicola* during burrowing and to compare the mechanism with that of other animals, in particular bivalve molluscs.

MATERIAL AND METHODS

Observations were made of the burrowing of *Arenicola* of 15–20 cm. length both at Hull and at the Marine Biological Laboratory, Millport, using specimens which would burrow rapidly. Direct visual observation of burrowing into sand could be made from above or from the side, through the glass of an aquarium tank. The latter was largely, but not always, unrewarding as even when the worm was close to the glass a thin layer of sand could obstruct detailed observation. Accordingly a technique (Trueman, 1966a) of continuously recording the pressure imparted to the sand by a burrowing worm was further developed by use of a more sensitive pressure transducer (Statham, Model P 23 BB, maximum sensitivity 0.4 cm. pressure/cm. pen deflexion) which was coupled to a multichannel pen recorder. Both instruments were obtained from E. & M. Instrument Company Inc.

Worms were allowed to burrow over a glass tube (3 mm. bore) buried in the sand with its external opening covered by a coarse nylon mesh to prevent entry of sand grains. This was connected by pressure tubing to the transducer, and pressure applied to the adjacent sand either by a plunger or by an *Arenicola* burrowing caused a negative response. The explanation of this may lie in the dilatant properties of the sand (Chapman and Newell, 1947), for the applied pressure disturbs the packing of the sand-water system and tends to cause water to be drawn in. In a full account of this technique (Hoggarth and Trueman, 1966) it is emphasized that all recordings must be interpreted by direct visual observations but that with this proviso it serves as a useful method of determining the activity of an animal, invisible beneath the sand yet without any obstruction by electrodes. Although burrowing was recorded in this manner for about 50 worms, direct observations of burrowing movements were only satisfactorily made on 5 occasions when the events were marked on the recording by means of a manually operated key. Coelomic pressures during burrowing were recorded as previously with a Bourdon transducer obtained from the E. & M. Instrument Company Inc. (Trueman, 1966a).

EXPERIMENTAL RESULTS

The recording of external pressures derived from an *Arenicola* burrowing in sand covered by several cm. of water consists of a series of negative pressures whose amplitude varies with the distance of the worm from the recording device. These pressures were observed to correspond to the swelling of the anterior segments and to a marked increase in the turgidity of the entire trunk region (Fig. 1a).

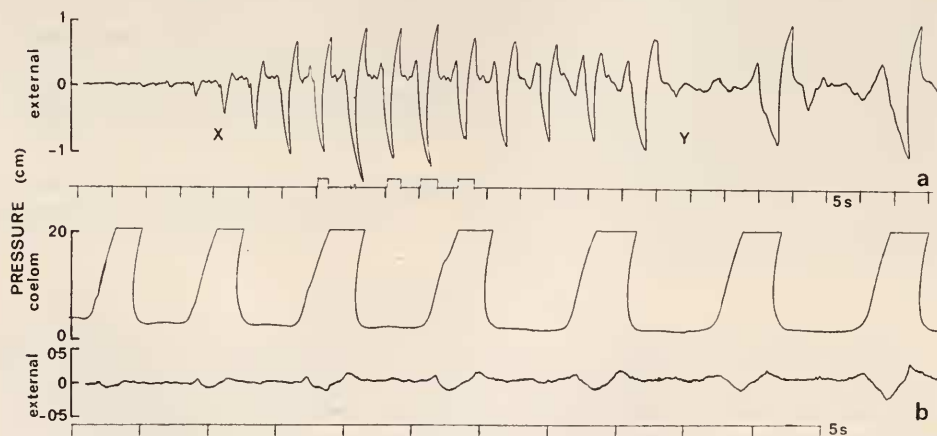


FIGURE 1. Recordings of the pressures produced by *Arenicola* in sand (external) and in the coelom during burrowing. a, sequence from the commencement of burrowing (extreme left) showing gradual increase in amplitude of the negative swings as penetration proceeds (at X) and the reduction of their frequency (at Y) after 6 branchial segments have passed into the sand. Visual observations of the swelling and turgidity of the anterior segments are indicated above the time trace. b, simultaneous recordings of coelomic and external pressures, commencing with four anterior segments beneath the sand. Lower amplitude of the external pressures due to greater distance from the recording device; flat tops of the coelomic pressure trace caused by saturation of the recorder.

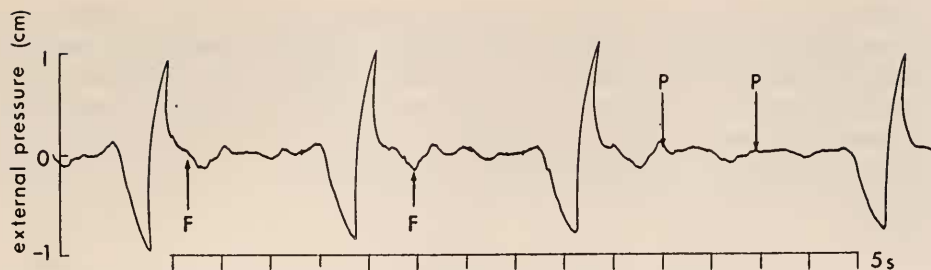


FIGURE 2. Recording of the pressures produced in sand by *Arenicola* when burrowing against glass with the trunk almost completely beneath the surface. Flanging (F) and proboscis eversion (P) were marked by direct observation of the anterior segments.

Synchronous recordings demonstrate that the negative pressures correspond to the pressure peaks in the coelom (Fig. 1b). At the commencement of burrowing the latter increase in amplitude with penetration (Trueman, 1966a; Fig. 6) and a similar feature occurs in respect of the negative pressures (Fig. 1a, X). This indicates that until a firm anchorage is obtained, maximum pressures are not exerted on the substrate.

The external pressure recorded fluctuates continuously between the negative peaks and it has not been possible to interpret these changes in detail. The most marked positive peak, following immediately after the negative pressure, may be due to the dilatant properties of the sand-water system. Proboscis eversion and the occurrence of flanging were marked by visual observations, through the side of a glass tank. Flanging (Fig. 3b) was most clearly observed on the first three trunk segments where the fleshy parapodial ridges each form an annulus which may be raised suddenly into a sharply projecting flange (Wells, 1944, 1961). Flanging and proboscis eversion were never observed at peak pressures but occurred between these (Fig. 2). Conversely the anterior 4 or 5 segments became very dilated when the maximum pressures were recorded (Fig. 3a). High pressures were clearly not synchronized with proboscis extrusion nor was there any apparent forward movement of the head of the worm at this phase of digging activity. It was previously (Trueman, 1966a) considered likely that the high coelomic pressure contributed to forward movement of the head of the worm but in the light of the present observations this appears to be incorrect.

After *Arenicola* has burrowed for 1 to 1½ minutes the frequency of the negative pressures often shows a marked reduction (Fig. 1a, Y). When recording the coelomic pressure a similar feature was observed and was interpreted as being due to the lack of development of the full muscular power of the worm, possibly because of fatigue (Trueman, 1966a). Waves of peristaltic contraction pass forward along the trunk during burrowing and develop into pressure peaks upon reaching the anterior segments. As burrowing proceeds each peristaltic wave does not produce high coelomic pressures or dilation and accordingly the negative pressures also occur less frequently. Proboscis extrusion and flanging continue, however, throughout the interval between maximum pressures. The proboscis effects the initial entry of the worm into the sand by a scraping action (Wells, 1961) and very likely continues to scrape away the substrate when more deeply burrowed. Re-

peated proboscis extrusion between pressure peaks is thus probably related to the progression of the worm. The resistance of the substrate to penetration increases with depth of burial (Trueman, Brand and Davis, 1966b) and the longer interval between pressure peaks allows time for more extrusions of the proboscis and extension of the head. During studies of burrowing by bivalves similar observations have been made, indicating that the amount of probing by the foot increases with depth of burial (Trueman, Brand and Davis, 1966a).

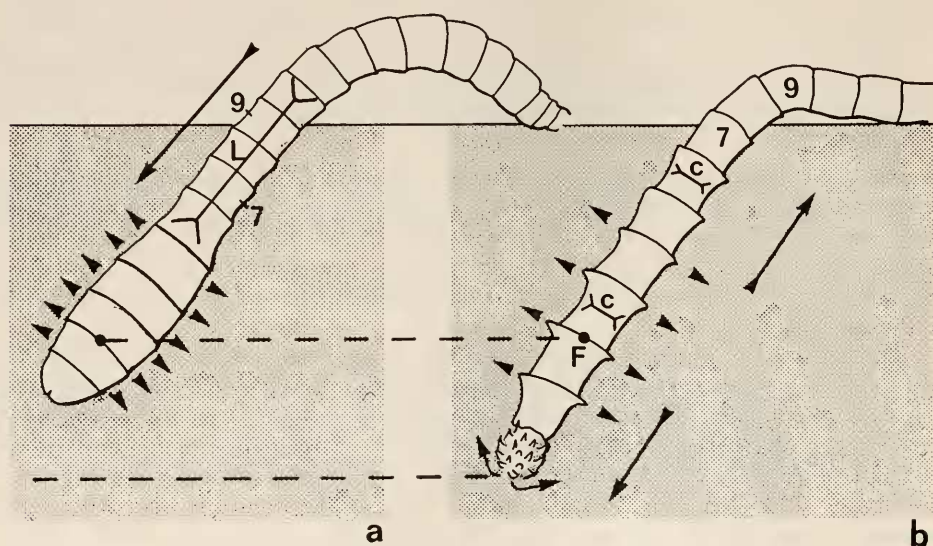


FIGURE 3. Diagram of two successive stages of burrowing of *Arenicola*. a, shows the anterior segments dilated to form an anchor (arrowheads), allowing the worm to penetrate the burrow (solid, tailed arrow) on contraction of the longitudinal muscles (double arrow, L). b, shows the flange anchor (arrowheads) and eversion of the proboscis (solid arrow). b, immediately follows a, at the fall of coelomic pressure, and involves elongation by the contraction of circular muscles (double arrow, C). Provided the flanges afford an anchorage, e.g., at F, on the second chaetigerous annulus, the head pushes forward and the posterior trunk segments retract from the burrow (solid, tailed arrows). Movement between a and b is also indicated by broken lines drawn between comparable parts of the worm and by the numbering of the segments.

BURROWING ACTIVITY OF *ARENICOLA*

On the basis of recordings (Figs. 1 and 2) and direct observations it has been determined that two principal conditions of the anterior trunk segments occur successively during burrowing activity. These are first, dilation, caused by the high coelomic pressures and secondly, flanging, accompanied by proboscis eversion (Fig. 3). Both of these conditions involve the anchorage of some part of the anterior region of the worm and in a normal burrowing sequence the type of anchorage alternates between the dilation anchor (Fig. 3a) and the flanging anchor (Fig. 3b).

The peristaltic wave passing forwards along the trunk forces coelomic fluid into the head with the contraction of the circular muscles posterior to segment 7 (Fig.

3a). This causes some increase in coelomic pressure, partial dilation of the most anterior segments (Trueman, 1966a) and is immediately followed by the contraction of the longitudinal muscles of the trunk. This brings about maximum dilation and a firm anchorage of the head, so allowing the posterior of the trunk to be pulled forward into the burrow. The effect of the head segments exerting pressure on a dilatant substrate is to make the sand-water mixture more resistant so that the chaetae can grip and the body-wall adhere to form a firm anchor. This stage of burrowing is equivalent to that described by Wells (1961) as an "anti-seagull" reflex, which he demonstrated by allowing a worm to burrow down the stem of a large glass filter funnel, the stem being closed by rubber tubing and a clamp. When the *Arenicola* was halfway into the stem, pulling the hinder end backwards caused the dilation of the anterior segments and resulted in a tenacious grip. This experiment has been repeated with a pressure transducer attached to the coelom and gave rise to high internal pressures which persisted while the hind end was being pulled.

In normal burrowing the high coelomic pressure and the dilation anchor are sustained by the contraction of the longitudinal muscles for not more than 2 seconds, being followed by the relaxation of these muscles and the contraction of the circular fibers so causing elongation of the worm. This elongation appears on the surface of the sand as a re-emergence of the posterior trunk segments from the burrow as the pressure drops (Trueman, 1966a). Contraction of the circular muscles completely eliminates the dilation anchor but this is replaced by the flanging anchor (Fig. 3b). This anchorage allows the second or third chaetigerous segment to remain static at elongation of the worm so that the segments behind will be pushed backwards from the burrow and those in front forwards into the substrate as the proboscis everts. This condition is shown diagrammatically in Figure 3b where the second annulus is arbitrarily taken as a fixed point about which movement backwards and forwards occurs. Wells (1954), in a detailed account of the mechanism of proboscis movement, considered that the head of *Arenicola* narrows and lengthens during the first stage of proboscis extrusion. This is in accord with the observation that eversion takes place when the dilation anchor is lost as the worm elongates.

The burrowing activity of *Arenicola* consists of the following stages: (1) Probing forward by the head, proboscis eversion obtaining initial penetration into the sand with no large pressures recorded. (2) Several segments buried, allowing a dilation anchor to form (Fig. 3a) with accompanying high pressures and the pulling forward of the worm into the burrow. (3) Relaxation of longitudinal and contraction of circular muscles, resulting in the lengthening of the worm and the production of the flange anchor (Fig. 3b). Further penetration of the substrate is then obtained by proboscis extrusion. (4) The second and third stages are repeated cyclically until burial is complete.

High coelomic pressures correspond to stage (2) but as the worm elongates during the third stage, the pressure drops sharply to the equivalent of little more than 2 cm. of water. The function of the high pressure is both to obtain an anchorage and to compact the sides of the burrow. External pressure negative recordings of *Arenicola* in normal U-shaped burrows show occasional strongly negative pressures, comparable to those recorded during digging, which suggest that high

coelomic pressures are used in the natural habitat, possibly to consolidate the burrow wall. Somewhat similar observations have been made in respect of burrowing in the earthworm (Roots and Phillips, 1960).

DISCUSSION

The digging activity of bivalve molluscs that burrow into soft substrates, such as *Cardium*, *Donax*, *Anodonta* or *Ensis* (Trueman, 1966b; Trueman *et al.*, 1966a), makes an interesting comparison with that of *Arenicola*, for all are well adapted for

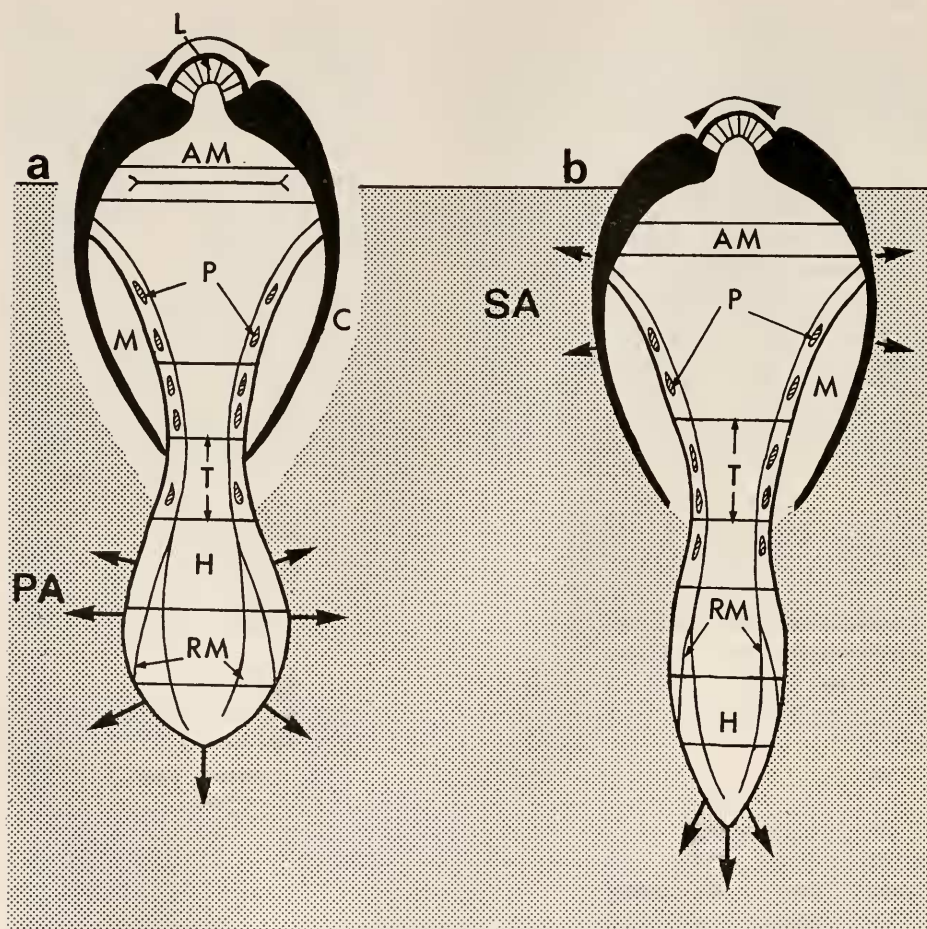


FIGURE 4. Diagram of two successive stages of burrowing of a generalized bivalve mollusc showing pedal (PA) and shell (SA) anchorages (arrows). a, valves adducted (double arrow, AM) producing pedal dilation and a cavity (C) in the sand around the valves. Contraction of the retractor muscles (RM) then causes the shell to be pulled down. b, valves reopened and pressed against the sand by the elasticity of the ligament (solid, double arrow, L) holding the shell fast when contraction of the protractor (P) and transverse muscles (T) causes pedal protraction. AM, adductor muscle; H, pedal haemocoel; M, mantle cavity.

burrowing. The latter has an essentially single coelomic system in contrast to the double system of the bivalves, which consists of the haemocoel, the hydrodynamic equivalent of the coelom in *Arenicola*, and the pallial system. Many bivalves thus have the advantage of being able to eject water from their mantle cavity during digging to loosen the sand adjacent to the shell (Fig. 4a, C). In both the thrust used in initial penetration is limited by the weight of the animal since any force in excess of the weight causes the animal to be pushed back from the sand. Further penetration of a bivalve consists of a series of step-like movements, each termed a "digging cycle," which were well recorded by Quayle (1949) in a study of the digging movements of *Venerupis*. Each digging cycle involves the integration of adduction and the reopening of the valves with retraction and protraction of the foot. Adduction causes high pressure in the haemocoel and as a consequence the foot becomes swollen to form a pedal anchor (Fig. 4a) (Trueman, 1966b). Immediately after adduction the retractor muscles, equivalent to the longitudinal muscles of *Arenicola*, contract, pulling the shell down and sustaining

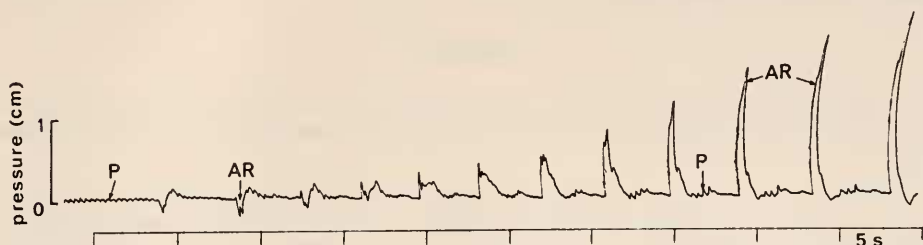


FIGURE 5. Recording of the pressures produced in sand by the burrowing of *Macra subtruncata*. At the commencement the bivalve is lying on the sand and the foot penetrates by probing (P). A succession of adductions of the valves and pedal retractions (AR) follow, giving first (left) negative swings, when the foot alone is beneath the sand, to be replaced by large positive pressures (right) when the valves have entered the sand. These are caused by ejection of water from the mantle cavity at adduction.

the pedal pressure and anchorage. Subsequently the opening moment of the hinge ligament opens the valves and presses them against the substrate (Fig. 4b) so forming a shell or secondary anchor. This holds the animal firmly whilst the foot extends by contraction of the protractor and transverse pedal muscles, which in this respect are the equivalent of the circular muscles of the body wall of *Arenicola*. The pedal and shell anchors of a bivalve correspond to the dilation and flange anchors of *Arenicola*, respectively.

The entire pattern of burrowing activity of a bivalve as recorded by the external pressures (Fig. 5) is very similar to that of the lugworm. It consists of a series of digging cycles each of which produces high pressure at adduction-retraction (AR). These are seen as negative pressures at the commencement of burrowing (Fig. 5, left) as in recording of *Arenicola*, but as depth of penetration increases (to the right, Fig. 5) and the shell enters the sand, water is ejected from the mantle cavity into the substrate and causes the succession of positive pressures (Hoggarth and Trueman, 1966). Between the "AR" peaks, when the shell anchor is applied, numerous probes (P) are made by the foot. These correspond to the pushing forward of the head of a worm from the flange anchor which occurs between each

negative pressure recorded. Although the structures used in digging in *Arenicola* and in bivalves are anatomically quite different there is a fundamental similarity in the mechanism that they employ.

Whilst discussing the burrowing of worms Clark (1964) considered that the method of burrowing used by all soft-bodied animals is essentially the same. He suggested that part of the body wall is first dilated to form an anchor while the head is forced into the substrate by contraction of the circular muscles, and that secondly the anterior end of the worm dilates to form a new anchor while the body is drawn downwards by contraction of the longitudinal muscles. These two anchorages correspond respectively to the flanging and dilation anchors of *Arenicola* or to the shell and pedal anchors of a bivalve. Essentially the same mechanism is used by other soft-bodied animals to burrow into sand, e.g., *Nephtys* (Clark and Clark, 1960), *Urechis* (Fisher and MacGinitie, 1928). Detailed knowledge, derived from continuous recordings of activity and internal pressures, is so far limited to *Arenicola* and members of the Bivalvia. It is hoped to extend these observations in the near future.

SUMMARY

1. The burrowing activity of *Arenicola* has been studied by means of direct observations and recordings of pressure changes both internally and in the adjacent sand.

2. Maximum coelomic pressures correspond to the swelling of the anterior segments to form an anchor (dilation anchor) which allows the posterior trunk segments to be pulled into the sand and the sides of the burrow to be compacted. This condition occurs alternately with the occurrence of flanges on the anterior segments as the worm elongates by contraction of the circular muscles.

3. The flanges tend to form an anchor (flange anchor) from part of the anterior region so that lengthening forces the head into the substrate, as the proboscis everts. At the same time the posterior trunk region undergoes some retraction from the burrow.

4. Essentially the same method is used by all soft-bodied animals to dig into sand, notably in bivalve molluscs. In this group a pedal anchor is formed by the foot becoming swollen by the hydrostatic pressure derived from adduction of the valves immediately before the shell is pulled down by the pedal retractor muscles. The shell is subsequently held still by the opening of the valves against the substrate (shell anchor) while the foot is protracted by the intrinsic pedal musculature.

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